

A REAPPRAISAL OF THE EARLY PERMIAN AMPHIBIANS *MEMONOMENOS DYSCRITON* AND *CRICOTILLUS BRACHYDENS*

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ABSTRACT. *Memonomenos dyscriton* Steen from the Autunian of Košťálov in Czechoslovakia is a temnospondyl amphibian of the family Archegosauridae, and not an anthracosaur as previously believed. Because of its close similarity to *Archegosaurus decheni* it is transferred to the same genus as a distinct species, *A. dyscriton* comb. nov. It appears to have been an inhabitant of a large stratified perennial lake in the Krkonoše-piedmont basin. Other material referred to the genus '*Memonomenos*' is not generically or specifically determinate. Another supposed anthracosaur, *Cricotillus brachydens* Case, from the Permian of Orlando, Oklahoma, is reidentified as large urocordylid nectridean material subjectively synonymous with *Crossotelos annulatus* Case. The North American genus *Archeria* represents the only lineage of anthracosaur (sens. Panchen) to survive into the Permian.

IN the final part of his *Fauna der Gaskohle*, published in 1901, Anton Frič described a new species of labyrinthodont, *Sclerocephalus credneri*, based on a specimen from the Permian of Ruprechtice in north-east Bohemia. To this taxon he referred several large labyrinthodont specimens from other localities in Bohemia including one slender skull, which he had briefly noted in an earlier publication (Frič 1896), from the Permian 'Brandschiefer' at Košťálov in north-central Bohemia. This locality had been known since 1869 and had produced several articulated skeletons of palaeoniscids and xenacanth sharks but no tetrapod fossils were found until the 1880s when Herr Benda, a schoolmaster, found the remains of two amphibians. One was the labyrinthodont skull mentioned above and the other was a urocordylid which Frič named *Ptyonius bendai*. Frič noted that the labyrinthodont skull was poorly preserved and that it was impossible to identify it with certainty.

In 1938 Steen designated this skull the type and only specimen of a new genus and species, *Memonomenos dyscriton*. In her description Steen did not place the genus within a systematic framework but described it under an 'incertae sedis' heading placed between descriptions of anthracosaurs and rhachitomes. At the time that Steen's account was published the accepted concept of labyrinthodont phylogeny was that of Watson (1919, 1926) in which the rhachitomous temnospondyls were derived from embolomorous precursors. Steen's description and its placing suggests that she considered *M. dyscriton* to be an intermediate form. Steen diagnosed *M. dyscriton* on the basis of the small tabular horns which, she suggested, were a relic of the larger anthracosaurian tabular horns. In her figure of the specimen she depicts a very small postparietal-supratemporal suture separating the tabular from the parietal, and the figure suggests the probable presence of intertemporal ossifications and marginally situated external nares. The skull is long and slender and similar in over-all proportions to those of some of the British Carboniferous eogyrinid anthracosaurs.

In his 'Review of the Labyrinthodontia', Romer (1947) demonstrated that anthracosaurs and temnospondyls were phylogenetically distinct in the Upper Carboniferous, and therefore that the Permian *M. dyscriton* had to belong to one group or the other. On the basis of Steen's description Romer placed *Memonomenos* in the anthracosaurs; he has been followed in this by subsequent authors (e.g. Panchen 1970), no other first-hand studies of the specimen having been made. One significance of this identification is that *M. dyscriton* purports to be the only determinate post-Carboniferous anthracosaur apart from the North American archeriids. Romer (1945) also referred some late Carboniferous anthracosaur material from Kounová, Czechoslovakia, to the genus *Memonomenos* as *M. simplex*.

The genus *Cricotillus* is based on a skull fragment from the Lower Permian of Oklahoma which Case (1902) described as *C. brachydens*. In 1911, Case doubtfully referred a second skull fragment from the same locality to this species. Case (1911) and Olson (1970) identify this material as belonging to a cricotid anthracosaur. Williston (1910) and Panchen (1970) have both suggested that it is not anthracosaurian but is skull material of the nectridean genus *Crossotelos*, which occurs at the same locality.

In 1971, the author was able to examine the type of *M. dyscriton*. This has permitted the following redescription and systematic reassessment of the specimen. The identity of the type material of *Cricotillus* is also critically discussed.

The following abbreviations are used in the specimen numbers given in this work: B.M. (N.H.), British Museum (Natural History), London; G.S.I., Geological Survey of India; K.U., Paleontological Museum, University of Kansas; N.M.P., National Museum, Prague.

SYSTEMATIC PALAEOLOGY

Class AMPHIBIA

Order TEMNOSPONDYLI

Superfamily ERYOPOIDEA Säve-Söderbergh, 1935, sens. nov.

Emended diagnosis. (Applicable to post-metamorphosis animals only.) Superficially crocodile-like amphibians growing to 3 metres total length. Preorbital snout elongated, in particular the nasals, frontals, and vomers. Premaxillae with a common medial suture almost as long as their outer antero-posterior length. Septomaxilla small and unornamented, situated within external nares, not extending on to the dermal skull roof. Lachrymal not contacting orbit margin, being excluded by the prefrontal-jugal contact anterior to the orbit. The centre of ossification of the jugal is level with the orbit and the jugal extends broadly anteriorly to suture with the lachrymal and prefrontal. No dorsal exposure of the palatine in the orbit margin. Inter-temporal bones absent. Pineal foramen retained in large individuals. Open otic notch present but proportionally small tympanic region, much of posterior edge of squamosal being convex and not bordering tympanum. The posterior edge of the ectopterygoid borders on the subtemporal fossa with no intervening pterygoid outgrowth. The palatine rami of the pterygoids narrow anteriorly and do not suture with the parasphenoid. The basisphenoid-ptyerygoid connection may be an articulating surface or a narrow suture but is not broadly sutured. Vertebrae rhachitinous, tending to stereospondyly in *Parioxys*. Where condition is known, twenty-three to twenty-four presacral vertebrae present.

Included families and genera. Eryopidae: *Eryops* (inc. *Glaukerpeton*), *Onchiodon* (inc. *Pelosaurus*), *Osteophorus*. Actinodontidae: *Actinodon* (inc. *Lysipterygium*), *Sclerocephalus*, *Cheliderpeton*. Archegosauridae: *Archegosaurus* (inc. *Memonomenos*), *Platyops*, *Prionosuchus*. Melosauridae: *Melosaurus* (inc. *Tryphosuchus*). Intasuchidae: *Intasuchus*, *Syndiodosuchus*. Parioxyidae: *Parioxys*.

Remarks. The superfamily Eryopoidea (also referred to as Eryopoideae by Säve-Söderbergh (1935) and Eryopsoidea by Romer (1947)) is ill-defined and has been very variable in its content, apart from the Eryopidae. Romer (1947) combined within it the Eryopsidae (correctly Eryopidae), the Dissorophidae, the Trematopsidae (correctly Trematopidae), and Zatracheidae (correctly Zatrachydidae). The genus *Parioxys* was included in the Trematopidae. This grouping of families was defined as being rhachitomous temnospondyls with otic notches, no intertemporal bones, and a fixed basisphenoid-pterygoid suture. Romer placed similar forms with a mobile basisphenoid-pterygoid articulation in another superfamily, the Micropholoidea, comprised of the Micropholidae, Archegosauridae (inc. *Melosaurus*), Chenoprosopidae, and Lysipterygiidae. The artificial nature of these two superfamilies soon became apparent. Langston (1953) demonstrated that the Chenoprosopidae belonged to the superfamily Edopoidea, while it also became clear that fusion of the braincase and pterygoids in temnospondyls was an ontogenetic phenomenon affected by size, age, and neoteny (Romer 1968, p. 77). By 1966 Romer had expanded his earlier concept of the Eryopoidea to include the Archegosauridae, the new Russian family Intasuchidae, the Melosauridae, and the Parioxysidae, the latter two families founded on the genera *Melosaurus* and *Parioxys* respectively. The Micropholidae was submergered within the Dissorophidae.

More recently, Bolt (1969), has proposed removal of the Dissorophidae, Trematopidae, and his new family Doleserpetontidae to a monophyletic superfamily, the Dissorophoidea, to which Boy (1972*b*) has since added the Micromelerpetontidae and the reinstated Branchiosauridae. However, no author has subsequently considered the nature of the Eryopoidea remaining after removal of the dissorophoids. The principal purpose of this work is redescription of some misidentified material but, rather than assign it to a superfamily which, by default, exists undiagnosed and with undefined content, I have attempted to establish the diagnosis and contents of a redefined Eryopoidea.

The superfamily as defined above is a group showing little variation in the fundamental interrelationships of bones, the principal diversity being in the relative proportions of the skull and the appendicular skeleton and in the type of dentition. The diagnosis serves to distinguish the Eryopoidea from the three other contemporary temnospondyl superfamilies, the Edopoidea, Trimerorhachoidea, and Dissorophoidea. However, because of good representation in the fossil record, the eryopoids show continuity with several descendant lineages included in the superfamilies Trematosauroidae, Rhinesuchoidea, and Capitosauroidae. Any attempt to demarcate a boundary between these superfamilies and their eryopoid predecessors is difficult and inherently arbitrary. It would be preferable to construct a phylogenetic framework within the Temnospondyli in which the eryopoid descendants would be included within the Eryopoidea or a comparable taxon. I have attempted neither this nor the establishment of any sister-group relationships in this paper as much more fundamental morphological and systematic work needs to be undertaken on the Temnospondyli as a whole, before cladistic relationships within this order can be established.

I have excluded the Zatrachydidae from the Eryopoidea, as this family of aberrant amphibians not merely has some very diagnostic autapomorphic characters, but lacks

some of the character states which would permit ready inclusion in the Edopoidea, Dissorophoidea, or Eryopoidea. Until a detailed study of the cladistic relationships of these superfamilies is made, it would be preferable to leave this family in an indeterminate position within the Temnospondyli.

Family ARCHEGOSAURIDAE Lydekker, 1885

Diagnosis. (Applicable to post-metamorphosis animals only.) Preorbital snout long and slender, narrowing sharply just anterior to orbits. Lachrymal contacts neither external naris nor orbit margin. Interfrontal absent. At level of orbit, jugal is no wider than the orbit itself. The parietal and supratemporal are antero-posteriorly elongate and the latter shares a long common suture with the squamosal. Otic notch small. Jaw suspensorium level with or slightly behind level of occipitals. Lateral line system present where detectable. Two pairs of anterior palatal vacuities present, the premaxillary vacuities and the internal nares, the latter situated three to four naris-lengths behind the external nares. Anterior ramus of pterygoid narrows to a point and does not contact vomer or parasphenoid. Marginal dentition of 40 teeth per jaw ramus. Palatine tusk followed by a long row of palatal teeth medial to maxillary teeth. Hyoidean ossifications may be present. Interclavicle large and rhomboidal, twice as long as broad. Clavicles large and ventrally expanded, overlapping interclavicle. Ilium not dorsally expanded. Humerus short, not massive.

Genus ARCHEGOSAURUS Goldfuss, 1847

Type species. *Archegosaurus decheni* Goldfuss, 1847.

Diagnosis. External naris always nearly terminal, preceded by no more than own length of premaxilla. No terminal tusk-bearing expansion and anterior end of snout or lower jaws. In adult, jaw suspension behind level of occiput. Premaxilla bears about eight teeth, and maxilla up to thirty marginal teeth. No uncinat processes on ribs.

Referred species. *A. ornatus* Woodward, 1905, *A. kashmiriensis* Tewari, 1960.

Archegosaurus dyscriton (Steen) comb. nov.

Text-figs. 1, 2

1938 *Memonomenos dyscriton* Steen, p. 240; fig. 26.

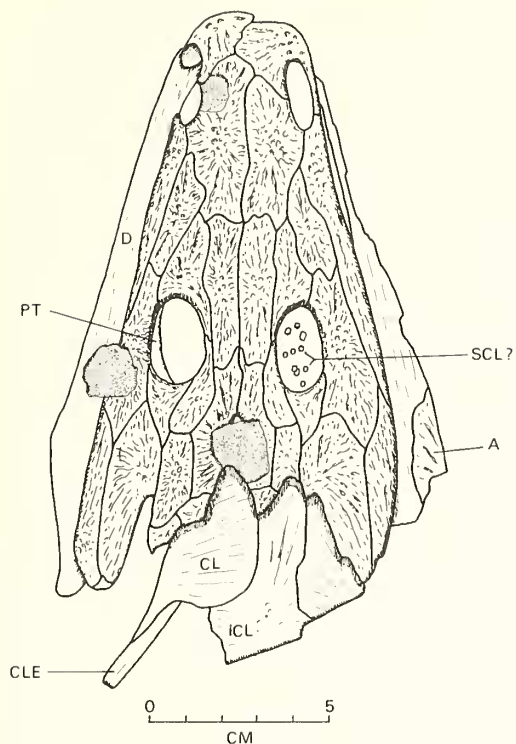
Material. Holotype and only specimen N.M.P. 6163 (referred to as Č.G.H. 6163 by Steen (1938) but the prefix Č.G.H. refers to a display catalogue).

Horizon. The Košťálov-Kalná horizon in the upper part of the Libštát Formation within the Krkonošepiedmont limnic basin in north-western Czechoslovakia (Holub 1972). The sedimentary sequence of this basin is believed to extend from basal sediments of Westphalian (Upper Carboniferous) age to uppermost horizons of Saxonian (Permian) age. The Košťálov-Kalná horizon is believed to be of Upper Autunian age (Andreas and Haubold 1975), and the Autunian is considered to be the lowest stage of the Permian by most European and North American workers. The stratigraphy and palaeoenvironments of the Krkonošepiedmont basin are discussed in relation to the amphibian material later in this paper.

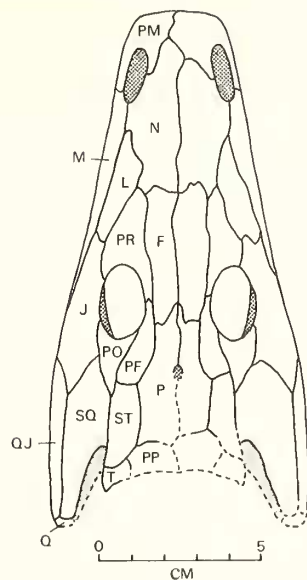
Locality. Košťálov, a village in the north-east Bohemian region of Czechoslovakia, 17 km east of Turnov and 36 km west of Trutnov.

Diagnosis. Similar to *A. decheni* but snout elongation occurs much more slowly relative to absolute size. Ratio of prepineal skull length: postpineal skull length of about 4:1:1 in skull of 144 ± 1 mm midline length. In *A. decheni* and *A. kashmiriensis* such a ratio occurs when the skull is between 60 and 80 mm long.

Description. The specimen N.M.P. 6163 (text-fig. 1) is preserved in a black, faintly laminated, bituminous limestone as a dorsoventrally crushed skull and pectoral girdle, visible in dorsal aspect. The mineralized bone is present and is pale brown in



TEXT-FIG. 1. *Archegosaurus dyscriton* (Steen) comb. nov., holotype, and only specimen as preserved. For the identity of the dermal bones of the skull roof, see text-fig. 2. Abbreviations: A, angular; CL, clavicle; CLE, cleithrum; D, dentary; ICL, interclavicle; PT, pterygoid; SCL?, possible sclerotic plates.



TEXT-FIG. 2. *Archegosaurus dyscriton* (Steen) comb. nov., restoration of the skull in dorsal and lateral aspect. Marginal dentition is hypothetical. Abbreviations for this text-fig. and text-fig. 6: F, frontal; IT, intertemporal; J, jugal; L, lachrymal; M, maxilla; N, nasal; P, parietal; PF, postfrontal; PM, premaxilla; PO, postorbital; PP, postparietal; PR, prefrontal; Q, quadrate; QJ, quadratejugal; SQ, squamosal; ST, supratemporal; T, tabular.

colour. There is no counterpart. As noted by Frič and Steen the preservation is not good and most of the surface ornamentation of the dermal bone had been lost. The radiating striations depicted on the cranial bones (text-fig. 1) are semi-diagrammatic and are intended to depict the centre of ossification of each bone rather than its precise appearance. The dorsal surface of the skull roof is sufficiently damaged that the bones are, in some instances, visible in horizontal section. Most sutures are clearly visible and, by tracing the interfaces between sets of radiating striations on neighbouring bones, the more obscure sutures can be traced. The skull is exposed in dorsal aspect and, although text-fig. 1 may at first suggest that the pectoral girdle overlays the skull, this is not so. Those parts of the skull which were superimposed on the clavicles and interclavicle had been crushed upwards and probably became detached when the specimen was re-exposed. The pectoral girdle is still below the level of the skull roof.

Skull. The skull is about 144 mm long along the midline. The central part of the back of the skull table is broken off, so that the accurate length cannot be measured; however, it can be deduced to within a millimetre or two. Most of the sutures are simple, many are undulating, but there is not the interdigitation of dermal roofing bones associated with large and adult labyrinthodonts. There is thus no reason to assume that the size of the specimen represents the normal adult size for the species.

Both premaxillae (interpreted as anterior parts of the lower jaws by Steen) are visible and show the animal to have possessed a narrow squared-off snout and large, slightly elongated external nares. No premaxillary teeth are preserved. The lachrymals do not contact either the external nares or the anterior margins of the orbits. Nasals, lachrymals, frontals, and prefrontals are all antero-posteriorly elongate, their appearance indicating that they have elongated during growth. Prefrontal and postfrontal meet medially to the orbit, excluding the frontal from the orbit margin. The jugal extends broadly around the outer edge of the orbit and is about as wide as the orbit itself. The postorbitals are backwardly extending triangular bones, longer than wide. Study of the radiating bone ossification patterns behind the orbit convinces me that intertemporal ossifications were not present (Steen indicated that they were possibly present), the supratemporals suturing directly with the postorbitals. Parietals and supratemporals are antero-posteriorly elongate. The pineal foramen is partly visible and is between 2 and 3 mm across. The tabular bears a small posterior projection as described by Steen, but the postparietal-supratemporal suture is longer than Steen indicated and the tabular is further from the parietal than she depicted (Steen 1938, fig. 26). The squamosal and quadratojugal extend backwards, so that the level of the jaw suspensorium is behind that of the occiput. Behind the left squamosal is a sliver of bone which might be a dorsally exposed part of a quadrate. In the outer margin of the left orbit is exposed a crescent of palatal bone which can only be interpreted as the dorsal surface of the palatine ramus of a triradiate pterygoid of the type associated with temnospondyls with large interpterygoid vacuities. In the right orbit are visible a few tiny plates of bone which may be sclerotic plates. Both rami of the lower jaw are visible, being spread out to either side of the skull, but little of their structure can be ascertained. Part of the anterior margin of the angular is visible on the right ramus. The general shape of the mandibles suggests that they were slender and not deep in the angular region. No teeth are exposed on the specimen.

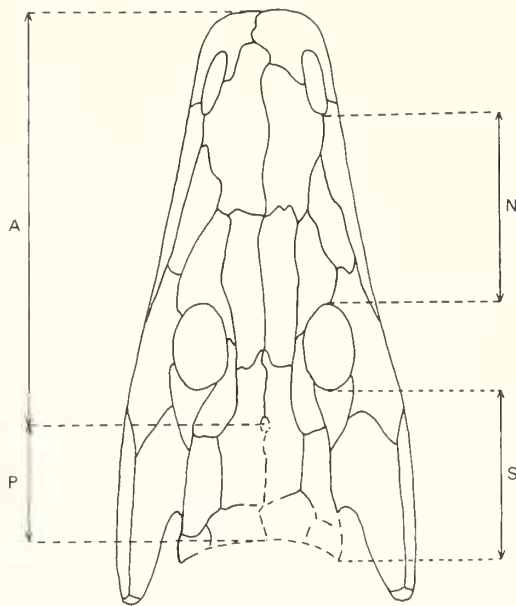
Pectoral girdle. This is exposed from the dorsal side and so no ornamentation is visible. The interclavicle is large and of rhomboidal type. It is only partly preserved but there is part of a broad posterior extension present. The clavicles are expanded ventrally and broadly overlap the interclavicle. Part of the left cleithrum is also present.

Remarks. From the description and text-figs. 1 and 2, it can be seen that N.M.P. 6163 is not an anthracosaur as defined by Panchen (1975). There are no intertemporals, no tabular-parietal contact, the external nares are large, oval, and not marginal and, most significantly, there were large interpterygoid vacuities. These characters indicate that the specimen is a temnospondyl. Characters which permit reference to the superfamily Eryopoidea include the long snout, the prefrontal-lachrymal-jugal configuration, the absence of intertemporals, and the small otic notches. The very slender

snout, jugals, and elongate skull table correspond to the proportions of a small skull of an archegosaur, and I can find no feature which would justify this specimen being retained in a genus separate from *Archegosaurus*. Our knowledge of *Archegosaurus* is based primarily on abundant material of the type species *A. decheni* Goldfuss from the Autunian of Lebach in the Saar region of West Germany. The only other described material now referred to this genus is that from the Permo-Carboniferous *Gangamopteris* beds of Kashmir, specimens of which have been described as *A. ornatus* Woodward, 1905 and *A. kashmiriensis* Tewari, 1960. Material from the Zone O Permian of European Russia has been listed as *Archegosaurus* sp. but not described (Olson 1957). Thus N.M.P. 6163 is contemporary with known *Archegosaurus* species in so far as correlations are reliable, and occurs within the known geographic range of the genus. Comparison of N.M.P. 6163 with material of *A. decheni* reveals no differences in the number and interrelations of the visible bones of the skull. The over-all proportions are similar, though not identical, to *A. decheni* of the same size and it is therefore suggested that N.M.P. 6163 is referable to the genus *Archegosaurus* and hence that *Memonomenos* be reduced in synonymy with *Archegosaurus*.

Specific identity. Intuitive observation of the skull of N.M.P. 6163 suggested that its snout was proportionately slightly shorter than in skulls of *A. decheni* of comparable size. The assemblage of *A. decheni* specimens from Lebach includes skulls from mid-line length 25 mm (Meyer 1858, p. 220) to at least 225 mm (B.M. (N.H.) R. 1785), and, over this size-range, the proportions of the skull change radically as noted by Meyer (1858) and Romer (1939). The small animals had very short snouts and probably fed on small pelagic or benthic animals by suction-gulping. This interpretation is supported by the presence of gill-raker ossicles in small specimens and also by an ossified basibranchial not found in large specimens, which is probably associated with gulping musculature. The largest known individuals had long slender gharial-like snouts bearing rows of pointed recurved teeth and must have been snapping piscivores living in a fish-rich lake (Boy 1972a). The relative length of the snout increases constantly with growth in *A. decheni* and a short morphometric study was undertaken to establish whether N.M.P. 6163 fell within the growth series of *A. decheni*. Measurements were taken from twenty-three skulls of *A. decheni*, fifteen in collections in the British Museum (Natural History) and eight from Meyer's figures of some of his better specimens. Data for *A. kashmiriensis* from Tewari (1962) was also incorporated, but the only specimen of *A. ornatus* lacks the anterior snout and could not be used in this comparison. Dimensions were taken between major features of the skull (e.g. edges of naris, orbit, or skull margin) and not between sutures, as the latter are rarely symmetrical and do not give comparable fixed points between specimens. Furthermore, many skull roofing bones have suture faces which are not perpendicular to their outer surfaces but are sloping, with the result that dorsal and ventral dimensions of a dermal bone may be different. The dimensions used are depicted in text-fig. 3, and the resultant measurements and ratios are given in Table 1. The number of Lebach specimens which could be measured usefully was limited to twenty-three by the requirement for the complete snout to be present.

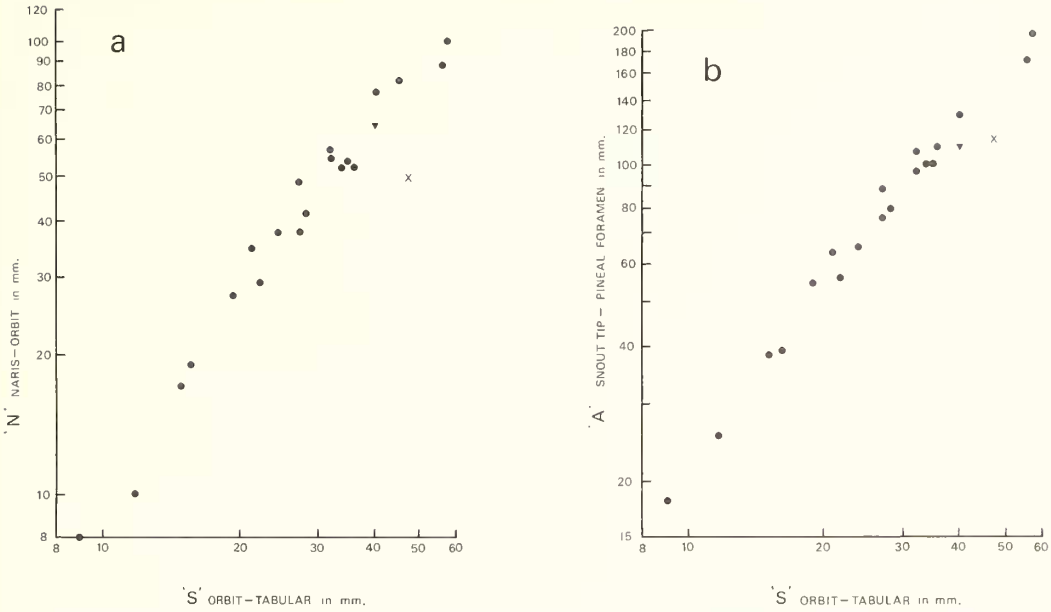
Dimensions S and P are parameters of the skull table, the slowest-growing part of the skull, and were used as a basis for comparison with dimensions A and N, which



TEXT-FIG. 3. *Archegosaurus dyscriton* (Steen) comb. nov., skull in dorsal view showing dimensions taken as basis for morphometric study.

TABLE 1. Cranial dimensions and proportions in three species of *Archegosaurus*. Data forming the basis of the plots in text-figs. 4 and 5. Dimensions as depicted in text-fig. 3.

	A+P	N	S	N:S	A	P	A:P
<i>A. decheni</i>							
Meyer, pl. 14, fig. 8	25	8	9	0.88	18	7	2.57
B.M. (N.H.) R. 42755	34	10	12	0.83	25	9	2.78
B.M. (N.H.) R. 1748	49	17	15	1.13	38	11	3.45
B.M. (N.H.) R. 1749	49	19	16	1.19	39	10	3.90
Meyer, pl. 14, fig. 12	67	27	19	1.42	54	13	4.15
B.M. (N.H.) R. 35798/9	69	29	22	1.32	55	14	3.93
B.M. (N.H.) R. 29001	70	—	—	—	57	13	4.38
B.M. (N.H.) R. 33069	78	34	21	1.62	63	15	4.20
Meyer, pl. 12, fig. 3	80	37	24	1.54	66	14	4.71
B.M. (N.H.) R. 40044	91	37	27	1.37	75	16	4.69
B.M. (N.H.) R. 40043	96	41	28	1.46	80	16	5.00
Meyer, pl. 12, fig. 5	103	47	27	1.74	87	16	5.44
B.M. (N.H.) R. 1787	116	57	32	1.78	97	19	5.11
Meyer, pl. 12, fig. 4	118	54	35	1.54	100	18	5.56
Meyer, pl. 12, fig. 1	120	52	34	1.53	100	20	5.00
B.M. (N.H.) R. 1298	126	55	32	1.72	105	19	5.55
B.M. (N.H.) R. 1786	129	52	36	1.44	108	21	5.14
B.M. (N.H.) R. 42806	152	76	40	1.90	128	24	5.33
Meyer, pl. 23, fig. 1	169	—	—	—	142	27	5.26
Meyer, pl. 11, fig. 5	—	81	45	1.80	—	26	—
B.M. (N.H.) R. 35806/7	180	—	—	—	152	28	5.43
B.M. (N.H.) R. 35796/7	205	87	57	1.53	172	30	5.73
B.M. (N.H.) R. 1785	225	100	58	1.72	193	32	6.03
<i>A. kashmiriensis</i>							
G.S.I. 18017	130	64	40	1.60	108	22	4.91
<i>A. dyscriton</i>							
N.M.P. 6163	144±1	50	48	1.04	116	28±1	4.14±0.16

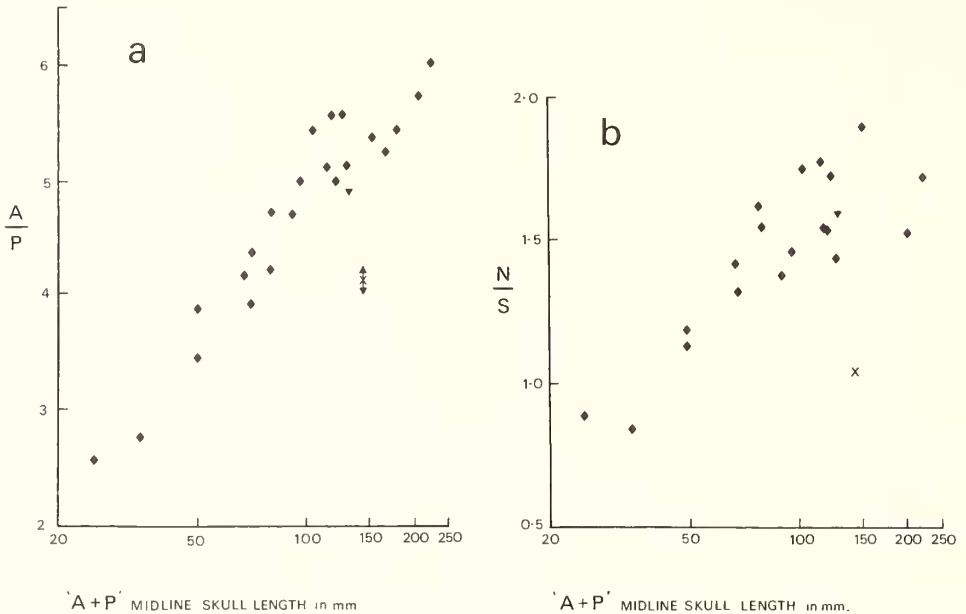


TEXT-FIG. 4. Bivariate plots of cranial dimensions of *Archegosaurus*. The scale on all axes is logarithmic and the dimensions on which the plots are based are tabulated in Table 1. The symbols used are as follows: ● = *A. decheni*; ▼ = *A. kashmiriensis*; x = *A. dyscriton*.

are parameters of the rapidly growing snout. Text-fig. 4 depicts bivariate plots of A and N against S on the abscissa. A clear result is obtained and the procedure was not repeated using P as in N.M.P. 6163, this dimension can only be estimated to within 2 mm because of damage to the skull table. It can be seen that, in both growth series, N.M.P. 6163 falls distinctly outside the sequence for *A. decheni*, while *A. kashmiriensis* falls within it. This is brought out more clearly in the comparisons in text-fig. 5. Here two different ratios of snout to skull-table dimensions, namely A:P and N:S, are plotted against absolute midline skull length (A + P). The dimension P had to be used for N.M.P. 6163 in this comparison and was estimated as 28 ± 1 mm, this degree of error being indicated in text-fig. 5a. The results were sufficiently pronounced to be worth using, even allowing for the uncertainty over the precise dimension of P. It can be seen that, for the *A. decheni* specimens, A:P is about 2.5:1 in a 25 mm skull and about 6:1 in a 225 mm skull. The ratio appears to increase linearly in direct relationship to the absolute size expressed logarithmically, with some scatter due to biological variability and the effects of post-mortem crushing. While the plot for *A. kashmiriensis* falls within the scatter for *A. decheni*, that for N.M.P. 6163 is very substantially outside. N.M.P. 6163 has an A:P ratio of 4.14 ± 0.16 in a skull of 144 ± 1 mm midline length, while the same proportions occur in *A. decheni* at between 60 and 80 mm midline length. Text-fig. 5b shows comparable results from plotting N:S against absolute size.

Thus it appears that N.M.P. 6163, while very similar to *A. decheni*, has a slower rate of allometric snout growth in relation to absolute growth and hence it has similar

proportions to an *A. decheni* of half the absolute size. It is thus morphometrically distinguishable from *A. decheni* and therefore I am retaining the specific name for this specimen, which is thus the holotype of the new combination *A. dyscriton*.



TEXT-FIG. 5. Bivariate plots of cranial proportions against absolute skull length in *Archegosaurus*. The scale on the abscissae is logarithmic and the dimensions and ratios used are tabulated in Table 1. The symbols used are as follows: \blacklozenge = *A. decheni*; \blacktriangledown = *A. kashmiriensis*; \times = *A. dyscriton*. In (a) the arrows bracketing the *A. dyscriton* plot indicate the range of possible ratios because of slight uncertainty over the postparietal dimension 'P'.

The apparently slower rate of snout elongation in *A. dyscriton* has several possible explanations, which cannot be verified without further material. As *A. dyscriton* is of similar shape to a smaller *A. decheni*; it could be a partly grown individual of a *decheni*-like animal with a much larger adult. The cranial sutures of N.M.P. 6163 show little interdigitation, which suggests that it was not a mature individual, supporting this hypothesis. Alternatively it could be an individual, mature or otherwise, of a species with a different feeding technique, which required a different snout morphology to that of *A. decheni*. Because of the poor correlation between Autunian limnic basinal sequences, it is not currently possible to determine whether *A. dyscriton* is earlier or later than *A. decheni* and, even if this were known, it might be of no consequence. If the two species do represent different feeding morphologies, they could have existed in parallel throughout the Autunian without any ancestor-descendant relationship, even in a general sense.

THE KRKONOŠE-PIEDMONT BASIN, STRATIGRAPHY AND
PALAEOENVIRONMENT

Neither Frič nor Steen give much information about the formation from which the Košťálov assemblage was obtained, but in recent years much stratigraphic work has been undertaken on the Permo-Carboniferous limnic basins of Czechoslovakia. A brief description of the Košťálov horizon and the palaeoenvironment of *A. dyscriton* is now possible.

The village of Košťálov is situated in the north Bohemian region of Czechoslovakia. Permian sediments of a limnic basin, the Krkonoše-piedmont basin, are exposed in this area. The exposed strata indicate an elongate basin extending about 50 km in an east-west direction and 20 km in a north-south direction, with the Košťálov locality in the western part of the basin. Sedimentation in this basin is now believed to have occurred principally during the Autunian (Andreas and Haubold 1975). Post-Autunian deposits have apparently been eroded over much of the basin, but Saxonian conglomerates follow the Autunian over parts of the eastern basin. Most of the sediments are of 'red-bed' type, reddish-brown mudstones, micaceous sandstones, and claystones, sometimes part of deltaic fans and always unfossiliferous. They indicate a semi-arid climate and a basin system which usually had little standing water in it. However, occasional 'grey' horizons also occur; these may include grey-green mudstone and siltstones, coal seams, copper ore, and, occasionally, bituminous marlstone such as the fossiliferous Brandschiefer at Košťálov. These horizons frequently serve as local stratigraphical markers and, because they were laid down in anaerobic and sometimes basic conditions, they are fossiliferous. They indicate the intermittent presence in the basin of a lake with humid, vegetation-rich surroundings.

Havlena (1964) has divided the sediments of the Krkonoše basin into four major sequences, namely the Stupná and Semily members which she identified as Stephanian, the Libštát formation identified as Lower Autunian, and the Lomnice member identified as Upper Autunian. However, recent biostratigraphical evidence suggests that the entire sequence is Autunian. Using footprint faunules, Andreas and Haubold (1975) identify the Stupná and Semily members as Lower Autunian, and the Libštát and Lomnice members as Upper Autunian.

Three horizons in the Krkonoše basin have produced tetrapod remains, almost all of which are undescribed. The Lower Autunian Stupná member includes the productive Ploužnice horizon which at the type locality of Ploužnice has produced a fauna of xenacanth, acanthodians, palaeoniscoids, and small temnospondyls, possibly *Branchiosaurus* sens. strict. The lower part of the Upper Autunian Libštát member consists predominantly of grey beds and is known as the Rudník horizon. At Rudník, a vertebrate fauna occurs in bituminous marlstone and, as at Ploužnice, consists of xenacanth, acanthodians, palaeoniscoids, and small temnospondyls. At the uppermost part of the Libštát formation is a sequence of mudstones and limestone nodules followed by the grey Košťálov-Kalná horizon. This horizon is extensive and, at the edge of the basin, it transgresses over earlier Palaeozoic rocks, suggesting that for this short period the lake within the basin was at its most extensive (Holub 1972). Within the unproductive grey beds are lenses of limestone and bituminous marlstone which contain the most extensive vertebrate fauna in the basin, although many of

the species are represented only by single specimens. There are two vertebrate-bearing localities, one at Horní Kalná, which has produced only palaeoniscoids, the other at Košťálov, which has produced xenacanth, acanthodians, palaeoniscoids, the lungfish *Ctenodus*, and four types of tetrapod. These are: *A. dyscriton* (represented by the single specimen redescribed in this paper); an undescribed temnospondyl specimen which Holub (1958) refers to *Cheliderpeton* (correctly, I believe); a specimen of a urocordylid amphibian described by Fritsch (1901) as *Ptyonius bendai*, and some small specimens which Holub (1958) refers to *Branchiosaurus* sp.

Holub (1972) interprets the Košťálov-Kalná beds as being formed during a humid phase of the Autunian, at which time the Krkonoše basin was filled by a large lake. Holub *et al.* (1975) note that very few horizons in the Autunian of Czechoslovakia have this character, and their palaeogeographic map of the Bohemian region in the late Stephanian and Autunian shows the central Krkonoše basin to be the second largest of only four small depositional areas indicative of perennial lakes. Thus the large lake environment seems to have been rare in this area at this time. The matrix in which the animal remains are preserved also supports the interpretation that this is a lake fauna. It is very carbon-rich, suggesting an anaerobic-preserving environment, and in section can be seen to be very finely laminated, suggesting no post-depositional disturbance of sediment by water currents or scavengers. The articulated nature of many of the vertebrate remains indicate little post-mortem transport or decomposition, but that the animals fell into an anaerobic environment immediately after death. All this suggests a large lake with an oxygenated circulating epilimnion inhabited by vertebrates and a stagnant anaerobic hypolimnion where they were preserved undisturbed after death. The only other Autunian assemblage in Europe which appears to have been a product of such an environment is that at Lebach. Boy (1972a) has reviewed the palaeoecology of the Lebach locality and concluded that it was the bottom of a large stratified lake with epilimnion and hypolimnion. Faunally, Lebach and Košťálov have some distinct similarities if the poor Košťálov assemblage is assumed to be representative. The two assemblages both contain a diversity of fish including xenacanth sharks and dipnoans, and both have the genus *Archegosaurus* which does not occur in other European Autunian assemblages. Actinodontid temnospondyls occur at both localities but are not restricted to this type of assemblage and are frequent in assemblages derived from shallow or ephemeral lakes.

In conclusion, it appears that *A. dyscriton* was an inhabitant of a large stratified perennial lake in a humid vegetation-rich basin. Such lakes were apparently very local and short-lived during the Autunian in Europe and it is likely that the genus *Archegosaurus* also lived in at least one other environment from which it could colonize such large lakes, perhaps large rivers.

THE TAXONOMIC STATUS OF 'MEMONOMENOS' SIMPLEX

Some of the material from the Stephanian of Kounová in Czechoslovakia was described by Frič (1885) as six species of the genus *Macromerion*. The type species *Macromerion schwarzenbergi* was based primarily on sphenacodont pelycosaur

material to which it now exclusively applies. Other material referred to *M. schwarzenbergi*, and material which formed the basis of *M. simplex*, was identified by Romer (1945) as belonging to an anthracosaurian labyrinthodont. He made this material the basis of a new combination *Memonomenos simplex*, referring Frič's species to the genus *Memonomenos* because the type species of the latter was the only apparent embolomerous anthracosaur from the Permo-Carboniferous of Czechoslovakia. The reference to *Memonomenos* was not based on any morphological criteria, as '*M.*' *dyscriton* consists of a skull and pectoral girdle while '*M.*' *simplex* was based on postcranial material, particularly ilia and vertebrae.

Panchen (1970) observed that the type of *M. simplex* was an ilium which, while being of labyrinthodont type, was not necessarily anthracosaurian and was quite possibly loxomatid. The only certainly anthracosaurian bones which Panchen identifies are an incomplete pelvis and a vertebral centrum of a large embolomere, both specimens being part of Frič's *M. schwarzenbergi*, neither being types. Thus the Kounová anthracosaur has no valid specific name, as pointed out by Panchen (1970), and, because *Memonomenos* has been shown to be a junior synonym of *Archegosaurus*, no valid generic name either. Pending discovery of further material from this area, the Kounová material is indeterminate at family level and below, and within the framework of systematics proposed by Panchen (1975), should be referred to as *incertae sedis* within the Infraorder Embolomeri. The material remains noteworthy as the latest known European embolomerous anthracosaur material, even though it is not determinate below infraordinal level.

THE AFFINITIES OF *CRICOTILLUS BRACHYDENS*

With the removal of '*Memonomenos*' the only anthracosaur genera identified from post-Carboniferous deposits are *Archeria* and *Cricotillus* from the Lower Permian of North America. *Archeria* is one of the better-known anthracosaurs, based on much material from Texas, Oklahoma, Kansas, and New Mexico. *Cricotillus* is known from two skull fragments from the Wellington Formation of Orlando, Oklahoma, which were first described by Case (1902).

Case (1902) described a fragment of an elongate snout K.U. 349, as *C. brachydens* and a poorly preserved posterior skull, K.U. 350, as *Trimerorhachis leptorhynchus*. In the same paper he described some postcranial material from the same assemblage as *Crossotelos annulatus*. In a later account, Case (1911) identified *Cricotillus brachydens* as a cricotid anthracosaur; *T. leptorhynchus* as indeterminate but possibly the same animal as *C. brachydens*, and *Crossotelos annulatus* as a nectridean. Olson has reviewed the fauna (Olson 1967) and the two skull fragments (Olson 1970) and has argued that the two specimens belong to a characteristic small cricotid anthracosaur for which the name *Cricotillus brachydens* is valid. In a paper written independently of Olson's latter analysis, Panchen (1970) doubts that the material is anthracosaurian but suggests, following Williston (1910, p. 271), that it could be cranial material of the nectridean *Crossotelos annulatus* which is frequent at the same locality. Panchen also reclassifies the embolomerous anthracosaurs into the families Eogyrinidae and Archeriidae based on diagnostic cranial morphology, and rejects *Cricotus* as the basis

of a family as it is not associated with cranial material and cannot be assigned to a family with complete certainty, although a few minor postcranial features suggest that it is an archeriid.

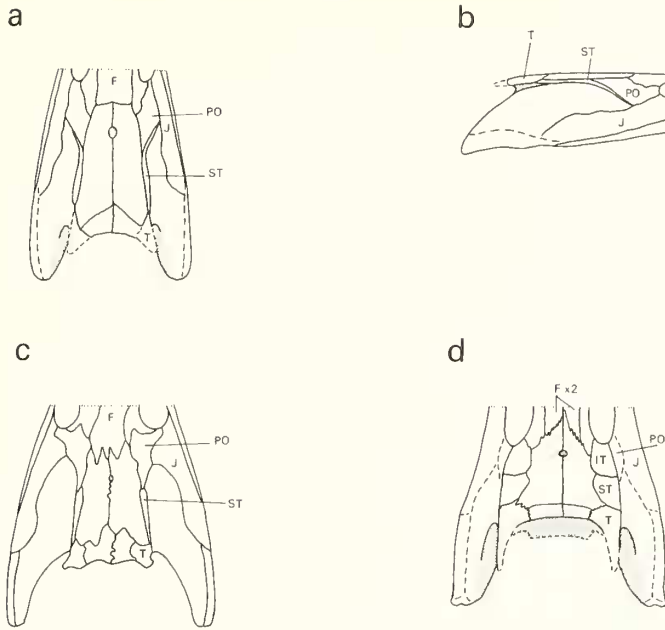
Olson's new description of the *Cricotillus* material includes several features which suggest that its affinities are with the urocordylid nectrideans rather than the anthracosaurs, despite his own interpretation. The following comparisons are based on descriptions of the urocordylid genera *Sauropleura* from Linton, Ohio (Steen 1931) and '*Urocordylus*', Nýřany, Czechoslovakia (Steen 1938), and on descriptions of *Archeria* material from Texas (Panchen 1970).

The skull table of K.U. 350 is noted by Olson (1970) to be labyrinthodont-like but no more so than that of urocordylids. Unlike other nectrideans but like anthracosaurs, urocordylids possess a distinct, possibly kinetic dorsal skull table, an otic notch, a posteriorly extending jaw suspensorium, and a similar complement of dermal roofing bones. Hence the general resemblance of K.U. 350 to labyrinthodonts extends to urocordylids. More specific resemblances occur. Olson (1970, fig. 1B) depicts a single medial bone anterior to the parietals. The possession of a single medial frontal is characteristic of urocordylids and does not occur in any known anthracosaur. Olson notes that the parietals are antero-posteriorly slender and that the pineal foramen is situated far forward between the parietals. The parietals are more slender than in any known anthracosaur, but no more so than in, for example, *Sauropleura marshi*, figured by Steen (1938, fig. 2E). The anterior position of the pineal is normal, both in urocordylids and in *Archeria*.

Olson notes splint-like temporal bones bordering the parietals. He identifies these with the intertemporals and supratemporals of anthracosaurs, but in all known anthracosaurs the bones are rectangular and the intertemporal extends between the postfrontal and postorbital, whereas in *Cricotillus* it apparently separates the postorbital and squamosal. Urocordylids, however, possess splint-like supratemporals of exactly the shape and position depicted in *Cricotillus*. *S. marshi* from Linton (Steen 1938, fig. 2E) shows a long slender extension of the postorbital corresponding to Olson's 'intertemporal' in *Cricotillus*, which could thus be this structure separated from the main body of the postorbital by a crack. The slender bones bordering the parietal thus correspond to the urocordylid but not to the anthracosaur condition (text-fig. 6). Olson notes that the tabulars in K.U. 350 would have contacted the parietals, a condition shared by urocordylids and anthracosaurs.

The dentition of K.U. 349 and 350 consists of spaced, recurved pointed marginal teeth. As Olson notes, these are unlike those of *Archeria* which are chisel-like, blunt, and closely appressed, and he makes this a diagnostic feature of *Cricotillus*. Steen (1938, fig. 3A) figures a palate of '*Urocordylus scalaris*' in which recurved pointed teeth can be seen to be present. The lower jaw of K.U. 350 is shallower than in anthracosaurs but like that of urocordylids, although this could be a size-linked feature.

The anterior skull fragment, K.U. 349, which forms the holotype of *C. brachydens*, was interpreted as a snout by Case and as part of the lower jaw rami by Olson. Case interpreted the ornamented bones as nasals wedged between maxillae. Olson notes that this is impossible and briefly considers an alternative possibility, namely that they are nasals wedged between premaxillae in an elongated snout anterior to the



TEXT-FIG. 6. Comparison of posterior halves of skulls of three Permo-Carboniferous amphibians. *a, b*, '*Cricotillus brachydens*' in dorsal and lateral aspect, based on figures and information given by Olson (1970). *c*, Urocordylid skull based on '*Urocordylus scalaris*' as figured by Steen (1938, text-fig. 2C). *d*, Archeriid skull based on *Archeria crassidisca* as figured by Panchen (1970, figs. 11b, 16a); the sutures represented by dotted lines are after Broom (1913) and Cope and Matthew (1915).

external nares, and that ventrally the snout is made up of slender vomers wedged between premaxillae anterior to the internal nares. He rejects this solution on the grounds that it would be a modification unlike that in any known tetrapod, consisting of a slender snout made up of premaxillae, vomers, and nasals with internal and external nares set far back at a broader base of the snout. Instead Olson prefers an interpretation that K.U. 349 is an anterior portion of the lower jaw rami made up of dentaries, splenials, and postsplenials. However, in '*U. scalaris*' (Steen 1938, figs. 2C, 3A) the nasals can be seen to extend forwards between the premaxillae and are almost completely anterior to the external nares which are set well back on the snout. The vomers are long and slender and extend to the anterior end of the snout and hence must be appressed between the premaxillae. The position of the internal nares is undescribed, but they are unlikely to have been anterior to the external nares. In *S. marshi* (Steen 1938, fig. 2E), a very slender-snouted form, the nasals also extend between the premaxillae as very slender bones and, although Steen depicts elongate narial cavities between nasals and premaxillae, the external nares must have been situated posteriorly next to the lachrymal. A snout of a large specimen of *S. marshi* would resemble that of K.U. 349 in this configuration of bones. I suggest therefore that K.U. 349 is, in fact, the anterior end of a snout and that it belongs to an individual

of similar skull size to K.U. 350 and does not represent lower jaws of a larger individual as Olson concludes. The two specimens, collected from the same locality, could have belonged to a single skull.

On the basis of the above interpretation of the morphology of K.U. 349 and 350, I suggest that they are parts of the skull of a large urocordylid nectridean. The skull, based on K.U. 350, has a length of 48 mm from the anterior edge of the orbit to the posterior edge of the jaw suspensorium. The largest '*Urocordylus*' skull from Nýřany (Steen 1938, fig. 1C) has a corresponding length of 37 mm, its jaw suspensorium being similarly elongated posteriorly. The growth series of skulls of '*U.*' *scalaris* depicted by Steen (1938, fig. 2A-C) shows proportional reduction in relative orbit size and elongation of the jaw suspensorium with growth. The size of orbit and length of jaw suspensorium in K.U. 350 are extensions of these trends. So, on the basis of their structure and proportions, the two skull fragments are consistent with what one would expect in a very large urocordylid.

Other material from the Orlando locality supports this interpretation. The vertebrae named *Crossotelos annulatus* by Case also belong to a very large urocordylid nectridean. The caudal vertebrae show the characteristic slender neural spines and fused haemal arches of nectrideans and the proportions of these structures and their terminal striations characterize them as being urocordylid rather than keraterpetontid, the latter having shorter neural spines and haemal arches. The size of the Orlando vertebrae and associated dorsal vertebrae indicate a much larger urocordylid than described from the Carboniferous. The dimensions of a large caudal vertebra of *Crossotelos* based on figures of Case (1911) are 3.0 cm total height and 0.95 cm length. This is twice that of the largest Nýřany '*Urocordylus*' in linear dimensions and suggests the possibility of skulls even larger than that of *Cricotillus*. Hence on the basis of postcranial material alone, it can be seen that a large urocordylid was present in the Orlando assemblage, so the presence of urocordylid skulls up to and above the size of *Cricotillus* could be anticipated.

In conclusion I suggest that *Crossotelos annulatus*, *Cricotillus brachydens*, and *Trimerorhachis leptorhynchus*, all first published by Case in 1902, all refer to fragments of a single species of large urocordylid nectridean and not an archeriid anthracosaur. *T. leptorhynchus* is a *nomen oblitum* as noted by Olson (1970, p. 360), while the other two binomina appeared simultaneously in 1902. As the *Crossotelos annulatus* material has been consistently referred to the Nectridea, this would, in the interest of stability, be the most appropriate binomen for the material and it is suggested that *Cricotillus brachydens* become the subjective junior synonym. Even the name *Crossotelos annulatus* may prove not to be definitive for this material, as direct comparison with the Carboniferous urocordylids may demonstrate that the Orlando animal is generically or even specifically identifiable with one of them.

DISCUSSION

Apart from the reduction in synonymy of two superfluous genera, the systematic reassignments made in this study alter our understanding of the diversity and distribution of the anthracosaurs, both chronologically and geographically.

Embolomeros anthracosaurs first appear as fossils in the Namurian rocks of Nova Scotia and Scotland (Andrews *et al.* 1977) but are known in their greatest diversity from Westphalian and Stephanian horizons in Europe and North America. Panchen (1970, 1975) divides the Infraorder Embolomeri into three families, the Eogyrinidae, the Archeriidae, and, more doubtfully embolomeros, the Anthracosauridae (Panchen, 1977). These families are primarily defined on the basis of cranial morphology associated with feeding, and for this reason the family name Cricotidae based on the skull-less *Cricotus* material was rejected by Panchen (1970). There is a great apparent diversity of eogyrinids in the Westphalian and Stephanian, material of this age from Czechoslovakia, the British Isles, Nova Scotia, and north-eastern U.S.A. being referred to nine or ten genera. However, discovery of more adequate comparative material might well reduce the apparent range of genera from the British Isles (*Pteroplax*, *Pholiderpeton*, *Eogyrinus*, and *Palaeoherpeton*) and also from north-east U.S.A. (*Leptophractus*, *Neopteroplax*, and *Eobaphetes* (not an anthracosaurid); Panchen (1977)). The only probable archeriid from the Carboniferous is *Cricotus* from the Stephanian of North America, and the only known anthracosaurid material of any age is the *Anthracosaurus* material from the Westphalian of the British Isles (Panchen 1977).

With the removal of '*Memonomenos*' and '*Cricotillus*' from the Embolomeri the only Permian material now known is North American and consists of some embolomeros centra, possibly eogyrinid, from the 'Prideaux pocket' of Texas (Romer 1963) and abundant material of the type archeriid *Archeria* from many localities.

Thus, on the basis of known material, it appears that the Eogyrinidae became extinct throughout their range in Euramerica at around the Stephanian-Permian boundary, while the Archeriidae, so far known only from North America, survived throughout the Wolfcampian in the form of the single widespread genus *Archeria*. The extinction of both families seems to be directly relatable to the decline of the respective environments which they inhabited. Most eogyrinids are associated with lacustrine deposits and appear to have been large piscivorous lake dwellers (Panchen 1970). In the British Westphalian coal measures eogyrinids are associated with diverse fish assemblages including osteolepidids such as *Megalichthys* and a limited characteristic assemblage of amphibians including the loxommatid genera *Baphetes* and *Megalocephalus*, the aïstopod *Ophiderpeton*, and the keraterpetontid nectrideans *Keraterpeton* and *Batrachiderpeton*. A later example of such a lacustrine fauna is that from Kounová in Czechoslovakia, of Stephanian age, where the indeterminate, probably eogyrinid, material is accompanied by *Ophiderpeton* and *Megalichthys* as well as transported remains of terrestrial tetrapods of Texas red-bed type (Romer 1945). The tetrapod-rich pond or small lake assemblages from the Westphalian D of Linton, Ohio, and Nýřany, Czechoslovakia, are each known from many hundreds of specimens, but at both, eogyrinids and loxommatids are rare components of the assemblage, while osteolepidids are apparently absent. *Ophiderpeton* is represented by a few tens of specimens at each locality but no strictly *Keraterpeton*-like material has been described from either, *Diceratosaurus* from Linton being a more amphibious keraterpetontid than *Keraterpeton* while *Scincosaurus* from Nýřany is not a keraterpetontid at all (Angela C. Milner, pers. comm.). It is therefore suggested that the eogyrinids formed part of a specialist lacustrine complex of amphibians and fish

which ecologically barely extended into coal swamp pool assemblages such as Linton and Nýřany. This eogyrinid-loxommatid-*Ophiderpeton*-*Keraterpeton*-*Megalichthys* complex does not apparently extend into the Permian at all, whereas most other families of tetrapods from Linton and Nýřany have Permian representatives. The demise of this complex during the Stephanian throughout Euramerica seems to have been due to the loss of continuity and reduction in number of large lakes in space and time to the extent that a continuity of populations could not be maintained. The Armorican orogeny in central Euramerica during the late Carboniferous had the effect of breaking up the pan-continental system of lakes, swamps, and forests into a series of valleys and basins, separated by fold mountains, particularly in European Euramerica. During the Early Permian, increasing deposition of red-beds followed by a cessation of limnic and estuarine deposition throughout Euramerica, suggests that progressive drying was taking place, due partly to further land uplift and consequent drop in the water table, and partly due to over-all global climatic change resulting from the termination of the late Palaeozoic Gondwana glaciation. In these circumstances large lakes would have become less frequent and more isolated and in time, as new lakes evolved, they would have been colonized from neighbouring smaller water bodies rather than from more distant large lakes. The few large fish-rich lakes of the European Autunian, faunally represented by localities such as Lebach, Košťálov, and certain Autun basin localities, have a characteristic amphibian fauna. The niches for large piscivorous amphibia are filled by eryopoid temnospondyls such as the long-snouted *Archegosaurus* and the shorter-snouted *Actinodon*, *Sclerocephalus*, and *Cheliderpeton*. These taxa are all absent from the Permian of North America where the principal large piscivorous amphibians appear to be trimerorhachoids such as *Trimerorhachis* and *Neldasaurus*. The simultaneous decline of eogyrinids across Euramerica and their apparent replacement by different taxa in different regions of Euramerica suggests that their demise was due to such a change in the physical environment followed by recolonization of the niche by other groups, rather than straightforward biological competition in a constant physical environment.

The Permian anthracosaur *Archeria* is characterized by a long snout bearing a specialized dentition of small, uniform, marginal teeth with horizontal chisel-like edges, set in continuous rows. Such a dentition gives a continuous surface for gripping or nipping small soft-bodied invertebrates rather than impaling fish. One can envisage *Archeria* probing into mud or vegetation with its long snout, gripping any moving object between two rows of such teeth. In localities such as the Geraldine and Briar Creek bone-beds, *Archeria* is associated with terrestrial and semi-terrestrial tetrapods such as *Dimetrodon*, *Edaphosaurus*, and *Eryops*, in conditions suggesting pools in bog deposits (Romer 1957). In other localities where *Archeria* occurs with other presumed aquatic genera, e.g. Archer City bone-bed and Rattlesnake Canyon, there is nevertheless a substantial terrestrial component of dissorophids and captorhinomorphs. These associations suggest that *Archeria*, though obviously aquatic was not, like the eogyrinids, a dweller in large lakes, but lived in smaller water bodies much closer to the terrestrial environment, such as deltaic pools and rivers. In such an environment its survival into the Permian would not have been imperilled until extremely dry conditions prevailed over equatorial Laurasia, as happened eventually in the Permian.

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